

Capelin larvae (*Mallotus villosus*) and community structure of zooplankton off the coast of northern Norway

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Capelin larvae (*Mallotus villosus*) and mesozooplankton were collected in May 2001 in the southern part of the Barents Sea. During the period of hatching and first feeding, capelin larvae experience high mortality rates. In order to understand the underlying mechanisms influencing larval survival, we monitored a selected site for 10 days using a variety of different sampling approaches. Hydrological parameters conductivity–temperature–depth–fluorescence (CTDF) were recorded and zooplankton samples obtained simultaneously using MOCNESS at three time periods. The mesozooplankton consisted essentially of copepods (85%), dominated by *Calanus finmarchicus*. The zooplankton community consisted of different assemblages derived from different areas (i.e. different water masses; Atlantic and coastal). Capelin larvae were found in surficial coastal waters. Copepod nauplii and *C. finmarchicus* were less abundant in coastal waters where small copepodites (such as *Acartia* spp. and *Temora longicornis*) were found together with early stages of coastal invertebrates that are possible prey for capelin larvae. We suggest that capelin larvae base their foraging on small prey organisms frequently found among the coastal zooplankton and that these larvae are less dependent on the propagation of the recruiting generation of *C. finmarchicus* present from April to June.

INTRODUCTION

Mortality in fish is most severe during the early life stages (Leggett and DeBlois, 1994; Houde, 1997; Huse and Toresen, 2000), so the evolutionary selection pressure to decrease the duration of this phase should be substantial. For successful reproduction, eggs and larvae of fish should be placed in a favourable habitat, with biological and physiochemical conditions that maximize the probability of survival through the susceptible planktonic phase (Laprise and Pepin, 1995). Such areas are characterized by abundant food, low predation pressure and suitable salinity–temperature conditions with circulation patterns that will ensure optimal survival conditions. The coastal area, where many fish species spawn (e.g. capelin), is likely to fulfil many of the above demands.

The Barents Sea capelin (*Mallotus villosus*) spend their entire life in the Barents Sea, spawning along the southern coasts and feeding as young and adults in the productive areas in the northern parts of the sea (Gjøsæter, 1998). Spawning occurs on near-shore shallow grounds north of 68°N from February to June, with the bulk spawning occurring in April and hatching in May (Gjøsæter, 1998). After hatching, the pelagic fish larvae are transported into the central part of the Barents Sea. During this period, they face heavy mortality. Hamre (Hamre, 1994) advocated that predation by juvenile herring (*Clupea harengus*) causes very high mortality of capelin larvae with the consequence that recruitment often fails. However, stock/recruitment relations for capelin show that there is also a substantial density-dependent regulation of the capelin recruitment in years when young

herring are not present (Fossum, 1992; Gjørseter and Bogstad, 1998). The food availability experienced by capelin larvae is poorly documented.

Capelin larvae (length 9–74 mm) caught in the Gulf of St. Lawrence fed on invertebrate eggs, cyclopoid copepods and diatoms (Vesin *et al.*, 1981), and Moksness (Moksness, 1982) found that capelin larvae reared in mesocosms fed on many prey species including polychaete larvae, but there are few studies on capelin early life history and feeding ecology from the field. Stomach analyses of capelin larvae caught simultaneously with the present study show that a variety of prey were eaten by capelin larvae, and invertebrate eggs, bivalves, copepod eggs, nauplii and copepodites from small copepods to cyphonautes were particularly frequent (Pedersen and Fosheim, in prep.).

Few zooplankton studies have been conducted in the coastal waters off Finnmark (Lie, 1965), but the species composition is most likely similar to coastal areas further south (e.g. Nordvestbanken and Malangen) where extensive information exists (Falkenhaus *et al.*, 1997b; Halvorsen and Tande, 1999). Copepods are the most abundant zooplankton in northern Norwegian shelf areas, other taxa comprise only 5–8% of zooplankton numbers. In these regions the abundance of the different prey species for capelin larvae changes with the season, but the most abundant species is *Calanus finmarchicus*, which peaks in abundance in May (Halvorsen and Tande, 1999) and produces nauplii that might serve as food for capelin larvae (Karamushko and Reshetnikov, 1994). From late June onwards this species appears to be numerically low compared to the previous month and is replaced by *Oithona similis* and *Microcalanus pusillus* as the numerically most important species (Falkenhaus *et al.*, 1997a; Tande *et al.*, 2000).

The strength of the recruiting generation of prey species varies both interannually and regionally in higher latitudes, and although the mechanisms responsible for this variability are not fully understood, similar ranges of variability are very likely to occur in the spawning habitat of capelin. Capelin larvae appear to be more adapted to sustain dilute prey fields and less linked to the annual recruitment period of *C. finmarchicus* compared to larvae of herring and cod (Pedersen and Fosheim, 2006). Nevertheless the overlap in time and space with their preferred preys during the larval period is relevant for their growth and survival rates in spring. In the present study we analyse the spatio-temporal structures in the physical and biological environment, in which capelin larvae are found during their period of hatching and first feeding off the coast of northern Norway in May 2001. The objective of the study is to relate gradients in capelin larvae abundance to water mass characteristics, and

provide evidence for spatial and temporal overlap between capelin larvae and their potential prey.

METHOD

The study area was located on the northern coast of Norway, towards the southern part of the Barents Sea (Fig. 1), and covered an area of 116×19 km (between $25^{\circ}29'–28^{\circ}48'E$ and $71^{\circ}01'–71^{\circ}18'N$) with bottom depths varying from 152 to 388 m (on stations). The study area was chosen because of high concentrations of capelin larvae detected by a MultiNet (MultiNet Midi; Hydro-Bios Apparatebau) during the initial part of the survey. During a period of 10 days in late May 2001 we covered the survey area at three time intervals (time 1, 18–21 May; time 2, 23–24 May; time 3, 26–27 May) (Fig. 1). Hydrography and fluorescence were obtained at each station from surface to bottom using a Sea-Bird 911 CTD (Sea-Bird Electronics Inc., Washington, USA) and a Seapoint Chlorophyll Fluorometer (Seapoint Sensors Inc., Exeter, USA). The study was designed to detect possible shelf edge effects on the abundance of capelin larvae and encompassed three main areas (A, B and C, see Fig. 1). A fourth area (D) was included in time 3 because of high concentrations of capelin larvae discovered during the first two coverages. The southern Barents Sea is influenced strongly by the inflowing North Atlantic Current (NAC) and Norwegian Coastal Current (NCC), which flows parallel north and eastward along the coast of northern Norway. The hydrography along the Norwegian coast north of $62^{\circ}N$ is fundamentally dominated by the interaction of two water masses: coastal water (from the NCC), with salinities below 34.5, and Atlantic water (from the NAC), with salinities higher than 34.95 (Rey, 1981). In a simultaneous sampling in the study area the hydrography was recorded by a horizontal CTD mounted on a SCANFISH and showed that the area was highly dynamic with water masses that were exchanged several times during the 10 days of sampling (Pedersen *et al.*, 2005).

Zooplankton samples were obtained by a MOCNESS (Wiebe *et al.*, 1976, 1985) with a 180 μ m mesh size net towed at 1.5 knots. Densities of zooplankton and capelin larvae (ind. m^{-3}) were calculated from 30 stations resolved with 20 m depth intervals down to 120 m. From each sample, capelin larvae were counted on board and stored separately in ethanol. The rest of the sample was preserved in 4% formaldehyde buffered with hexamin. A bactericide, 1,5-propane-diol (5% by volume) was added to the preservative. In the laboratory, the net samples of zooplankton were identified to the species level, where all specimens in aliquots of ~ 1000

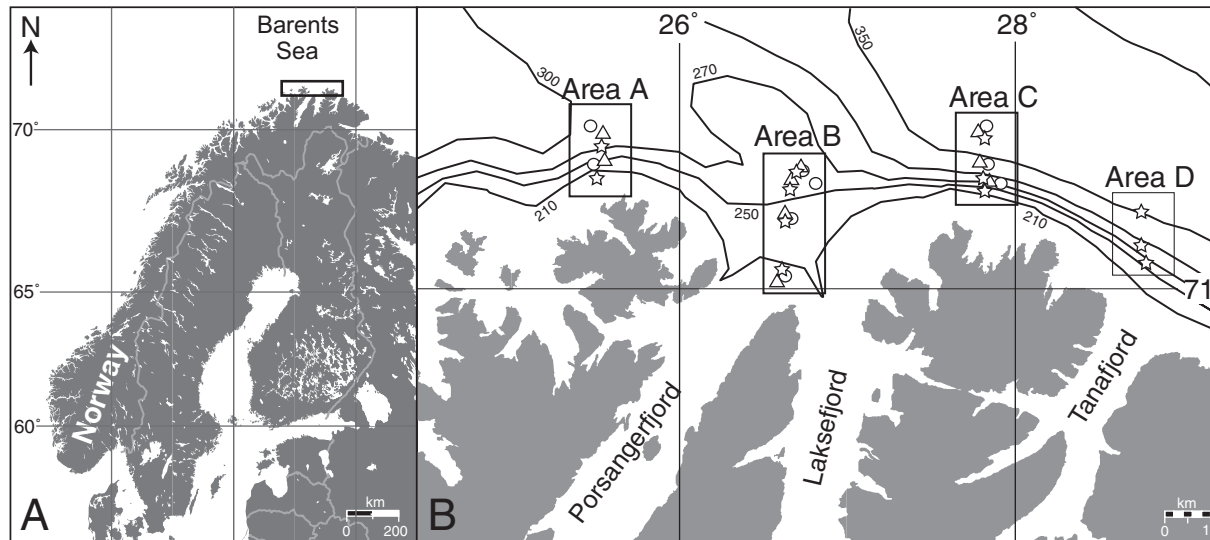


Fig. 1. (A) Index map of Scandinavia. (B) Study area in the southern Barents Sea with the three fjords, Porsangerfjord, Laksefjord and Tanafjord. Squares: Area A, B, C and D. Symbols: Stations in time 1, 18–21 May (○); time 2, 23–24 May (△); time 3, 26–27 May (☆) 2001.

animals were counted and identified under a Wild M3 stereomicroscope. No less than 1% of the original sample was identified. For species recorded in low numbers, larger sub-samples were employed. In addition to species identification, development stages were also noted. Some small copepods and copepod nauplii were probably lost due to the mesh size of 180 μm in the MOCNESS, and larger naupliar stages of the larger copepod species (i.e. *C. finmarchicus*) found in the study area were probably overrepresented in the copepod nauplii group.

Ordination analysis was carried out in order to investigate the association between environmental variables and species. We included data on zooplankton species from all stations, depth strata and all three sampling times, but only species present on more than 15% of the stations were included (i.e. present on more than 4 stations, out of 30) in the analyses. The original species abundance data were $\log(n+1)$ —transformed prior to analyses to downscale very abundant species and to reduce skewness. Environmental variables (salinity, density, temperature and fluorescence) were averaged for each depth interval (0–20 m, 20–40 m, 40–60 m, 60–80 m, 80–100 m and 100–120 m, abbreviated D10, D30 etc.) to enable statistical analyses relating species and environmental data. To investigate the influence of temporal and spatial scales on the species data we created dummy variables to study the effect of time (Time 1, 2 and 3), area (Area A, B, C and D, see Fig. 1) and depth (D 10, 30, 50, 70, 90 and 110 m). We also addressed the effect of phytoplankton by creating a dummy variable (dF) that separated stations into bloom or non-bloom stations. A bloom station was defined as a station where fluorescence was high, or highly heterogeneous through the water column, whereas a non-bloom station had low fluorescence levels in the whole water column. Applying these criteria we identified 15 bloom and 15 non-bloom stations.

After exploring the species data by correspondence analysis (CA), to reveal the main underlying pattern in species distribution and community structure (ter Braak, 1995), and generalized additive models (GAM) fitted to selected species (Hastie and Tibshirani, 1990), we applied redundancy analysis (RDA) to model the species data as functions of the measured environmental gradients (salinity, density, temperature and fluorescence) (ter Braak, 1995). The GAM was fitted on the two first CA ordination axes for capelin larvae, *C. finmarchicus* (CI, CII, CIII, CIV and CV), *O. similis* CI-V, *Oncaea borealis* F, *Oikopleura* spp., echinoderm larvae and the copepod *Acartia* spp. CIV-V. For capelin larvae abundance we also fitted a general linear model (GLM) by forward selection. Independent variables were time, area, depth, dF, temperature, salinity, density, fluorescence,

topographic depth and the interaction term topographic depth \times area. Topographic depth and its interaction term with area were used to reveal any potential effect of shelf edge induced processes such as jets and other phenomena that can be topographically steered. The statistical analyses were mainly done with the software CANOCO 4.5 (ter Braak and Smilauer, 2002), except for the GLM and post hoc tests that were done with SYSTAT 10.2 (SYSTAT Software Inc., 2002).

RESULTS

The mesozooplankton community consisted mostly of copepods (85% of all zooplankters), dominated by *C. finmarchicus* (53.7%), *O. similis* (11.8%) and copepod nauplii (9.6%). The copepods *Metridia* spp. CI-III (2.4%) and *O. borealis* F (1.8%) were found in lower proportions. Other groups were *Oikopleura* spp. (5.5%), euphausiids (4.4%), echinoderm larvae (2.2%) and capelin larvae (*M. villosus* \sim 1%). The remaining species (7.6%) are listed in Table I (updated from Fosheim *et al.*, 2005).

In the CA approximately 33% of the variance in the species data was accounted for by axes I and II (Fig. 2, Table II). Capelin larvae were associated with area B and surficial waters (D30, followed by D10 and D50) (Fig. 2, upper right). Capelin larvae were mostly associated with the copepods *Acartia* spp. (CI-III, CIV-V and F) and *T. longicornis* CIV-V as well as fish eggs, cyphonautes, *Limacina* spp., polychaete larvae, bivalves and cirripedia nauplii. However, only *Acartia* spp. CIV-V was sufficiently abundant (max value >50 ind.) to be included in further analyses together with the numerical important species. Capelin larvae were not associated with copepod nauplii, which was more associated with intermediate depths (D70 and D50) and blooming (dF).

The abundance profile of capelin larvae was positively correlated with ordination axis I (Fig. 3), which corresponds to a depth gradient. This means that the abundance of capelin larvae decreased with increasing depth. The abundance profile of capelin larvae was similar to that of *Acartia* spp. CIV-V, echinoderm larvae and *Oikopleura* spp. (Fig. 3). The isolines for the abundance of *O. similis* CI-V and *O. borealis* F were perpendicular to the isolines of the above groups, steadily decreasing with ordination axis II, clearly associated with the time component (Fig. 3). This means that the abundance of the latter two species had increased with time during the period of investigation. The abundance profile of copepod nauplii and *C. finmarchicus* CI-CII was positively correlated with ordination axis II (Fig. 4), declining with time, and opposite to what was seen for the cyclo-pods. The steepest abundance profile of *C. finmarchicus*

Table I: Zooplankton and capelin larvae (*Mallotus villosus*) collected with MOCNESS in the southern part of the Barents Sea in May 2001

Species	Stages	Abb	%
<i>Calanus finmarchicus</i>	CI	CfinC1	10.04
	CII	CfinC2	11.35
	CIII	CfinC3	16.76
	CIV	CfinC4	12.74
	CV	CfinC5	2.40
	Female	CfinF	0.40
<i>Calanus hyperboreus</i>	CII	ChypC2	0.01
	CIII	ChypC3	0.09
	CIV	ChypC4	0.05
	CV	ChypC5	0.01
	Copepoda	Nauplii	CopNau
<i>Metridia</i> spp.	CI	MetC1	1.17
	CII	MetC2	0.77
	CIII	MetC3	0.42
<i>Metridia lucens</i>	CIV	MlucC4	0.16
	CV	MlucC5	0.10
<i>Aetideus armatus</i>	Female	AearF	0.00
<i>Acartia</i> spp.	CI-CIII	AcaC13	0.09
	CIV-CV	AcaC45	0.31
	Female	AcaF	0.10
	Male	AcaM	0.06
<i>Temora longicornis</i>	CIV-CV	TlonC45	0.01
	Male	TlonM	0.00
<i>Pseudocalanus</i> spp.	CI-CIII	PseC13	0.32
	CIV-CV	PseC45	0.56
<i>Pseudocalanus acuspes</i>	Female	PacuF	0.21
	Male	PacuM	0.06
<i>Pseudocalanus minutus</i>	Female	PminF	0.05
	Male	PminM	0.01
<i>Microcalanus</i> spp.	CI-CV	MicC15	0.10
	Female	MicF	0.05
<i>Centropages</i> spp.	CIV-Ad	CenC4Ad	0.00
<i>Oithona similis</i>	CI-CV	OsimC15	4.81
	Female	OsimF	5.54
	Male	OsimM	1.49
<i>Oithona spinirostris</i>	CI-CV	OspiC15	0.75
	Female	OspiF	0.59
	Male	OspiM	0.07
<i>Oncaea borealis</i>	CI-CV	OborC15	0.20
	Female	OborF	1.77
	Male	OborM	0.13
<i>Evadne nordmanni</i>		Enor	0.00
<i>Euphausiacea</i>	Ova	EupOva	0.45
	Nauplii	EupNau	1.13
	Calyptopis	EupCal	1.65
	Furcillia	EupFur	1.18

<i>Sagitta elegans</i>	Juv	SeleJuv	0.02
	Ad	SeleAd	0.00
<i>Eukrohnia hamata</i>	Juv	EhamJuv	0.00
<i>Themisto abyssorum</i>		Taby	0.01
<i>Limacina</i> spp.		Lim	0.16
<i>Bivalvia</i>		Biv	0.10
Decapoda	Larva	DecLar	0.02
Echinodermata	Larva	EchiLar	2.18
Cirripedia	Nauplii	CirNau	0.09
	Cypris	CirCyp	0.17
Gastropoda	Larva	GasLar	0.02
<i>Oikopleura</i> spp.		Oik	5.54
<i>Fritillaria</i> spp.		Fri	0.14
Polychaeta	Larva	PolLar	0.14
Siphonophora	fragments	SipFrag	0.01
Cyphonautes		Cyp	0.01
Ctenophora	fragments	CteFrag	1.50
Ova var		OvaVar	0.26
<i>Medusae</i> spp.		Med	0.08
<i>Aglantha</i> spp.		Agl	0.13
<i>Chaetognatha</i> spp.	Juv	ChaJuv	0.09
Fish	Ova	FishOva	0.02
Capelin	Larva	Ma vi	~1

Abb, abbreviations used in statistical analysis; %, abundance of total in percent. $n = 30$ stations \times 6 depth intervals.

CIII was positively correlated with both ordination axes. The abundance of *C. finmarchicus* CIV and CV decreased from left to right along ordination axis I, opposite to that found for capelin larvae (Fig. 3).

In the RDA approximately 27% of the variance in the species and environment data was explained by axes I and II (Fig. 5). The species–environment correlation for axes I and II was strong (Table III). The first axis was correlated with salinity/density and the second axis was correlated with fluorescence (Fig. 5). The most important explaining factor underlying the zooplankton distribution was thus water mass characteristics, i.e. salinity/density and temperature. This gradient is clearly seen along the tilted environmental axis (from upper left to lower right in the RDA diagram, see Fig. 5) as the zooplankton species composition probably changed from a coastal community to an oceanic community. Capelin larvae were associated with coastal water, together with *C. finmarchicus* CI-CIII and *Acartia* spp. Copepod nauplii and *C. finmarchicus* CIV and CV were associated with more typical Atlantic water masses.

The general linear model of capelin larvae abundance obtained by forward selection included salinity, depth, fluorescence and time. The importance of salinity ($R^2 = 0.289$, P value <0.001) adds to our interpretation of

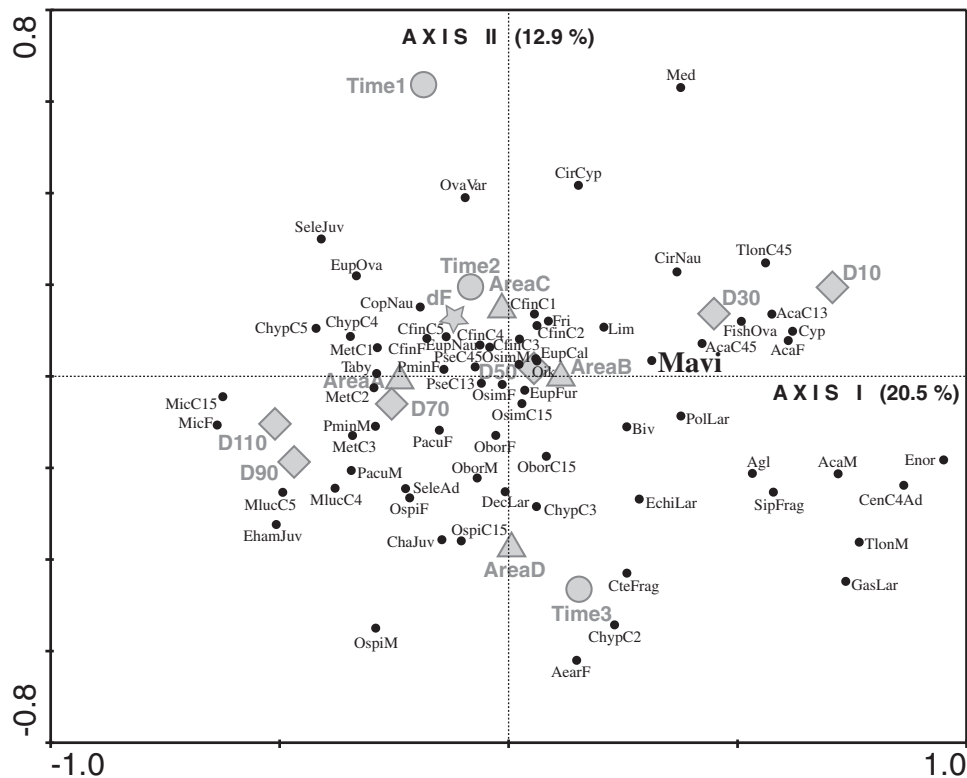


Fig. 2. Correspondence analysis (CA) ordination biplot of axes I and II relating abundance variations in zooplankton species to areas, depth intervals, times and blooming conditions ($n = 30$ stations \times 6 depth intervals). Species abbreviations explained in Table I.

Table II: Percentage of variance in species data explained and species–environment correlations by axes I–IV in correspondence analysis (CA) in Fig. 2

Axis	1	2	3	4
Percentage explained	20.5	12.4	6.9	4.0
Species–environment correlations	0.90	0.86	0.57	0.38

water mass characteristics as the major determinant of capelin larvae abundance and distribution in the RDA (Fig. 5). Maximum abundance of capelin larvae were found in the 20–40 m depth interval (= D30) and depth 10, 30 and 50 had significantly higher abundances than depth 90 and 110 (post hoc t -tests, P values < 0.05). The relationship between fluorescence and capelin larvae abundance was not significant ($R^2 = 0.011$, P value = 0.171). The abundance of capelin larvae increased from time 1 to time 2 to time 3 and a significantly higher abundance was found in time 3 than in time 1 (post hoc t -test, P value = 0.020). No effect of topographic depth (shelf edge induced processes) or blooming (dF) was found.

DISCUSSION

The zooplankton community in the southern part of the Barents Sea consists of different assemblages associated with different water masses. Typical oceanic, or Atlantic, species are clearly correlated with water that is more saline and warmer than the coastal water typical of Norwegian fjords (Rey, 1981). Oceanic species (such as *C. finmarchicus*) have population centres in the Norwegian Sea but are also found throughout the central Barents Sea (Arashkevich *et al.*, 2002; Falk-Petersen *et al.*, 1999). Typical neritic species such as *Acartia*, *Temora* and *Centropages* are usually more abundant in summer than in spring in fjords and near shore shelf water in northern Norway (Falkenhaug *et al.*, 1997b; Nielsen and Andersen,

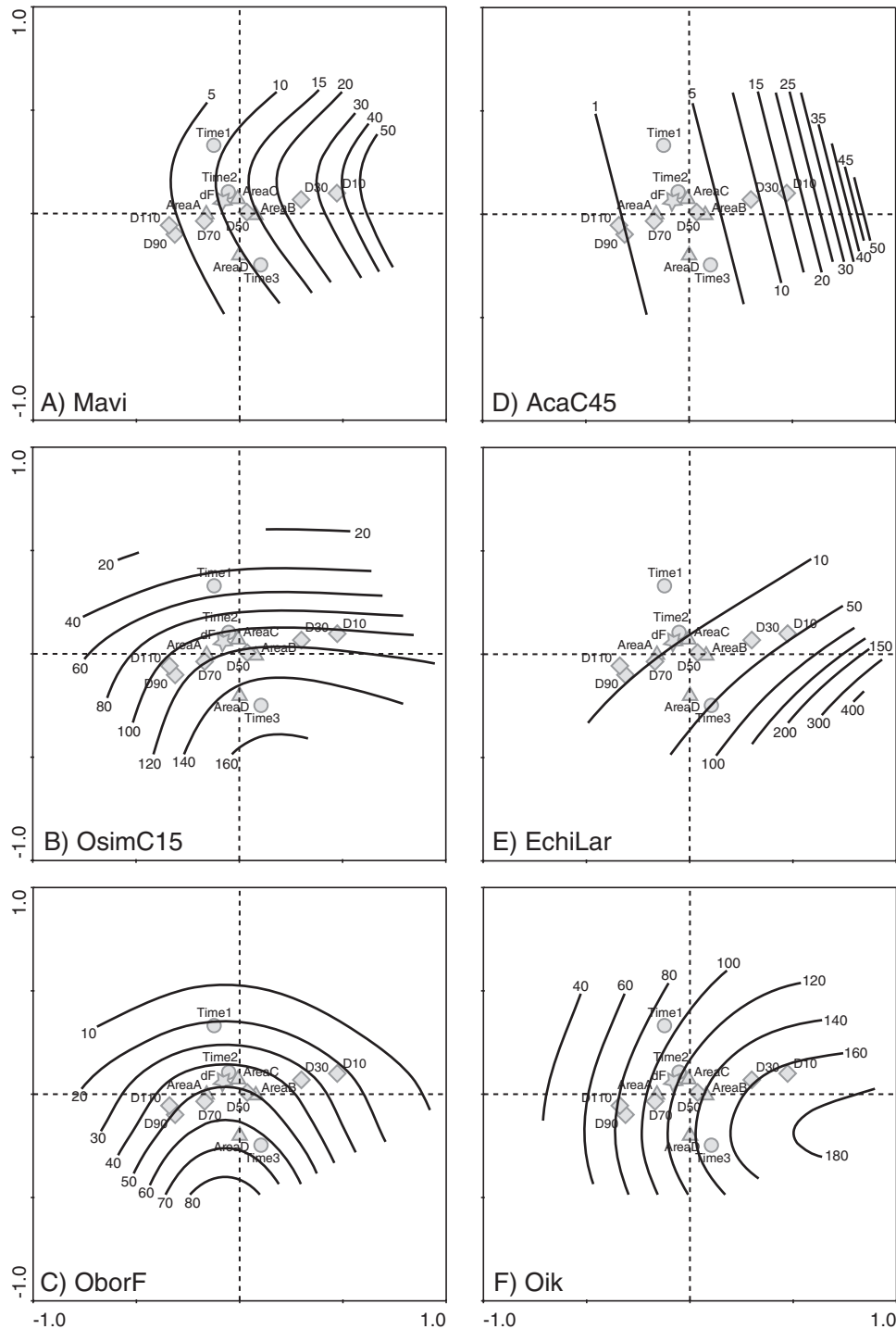


Fig. 3. Correspondence analysis (CA) ordination biplot of axes I and II with a generalized additive model (GAM) fitted to the abundance of (A) *Mallotus villosus*, (B) *Oithona similis* CI-V, (C) *Oncaea borealis* F, (D) *Acartia* spp. CIV-V, (E) Echinoderm larvae and (F) *Oikopleura* spp. ($n = 30$ stations \times 6 depth intervals). Species abbreviations explained in Table I.

2002). Although oceanic and neritic species have different population centres, their overlap in distribution is very much related to advection and water mixing on

the shelf. The zooplankton community in our study area was dominated by copepods and by species that are oceanic (i.e. Atlantic) in origin. *C. finmarchicus* was

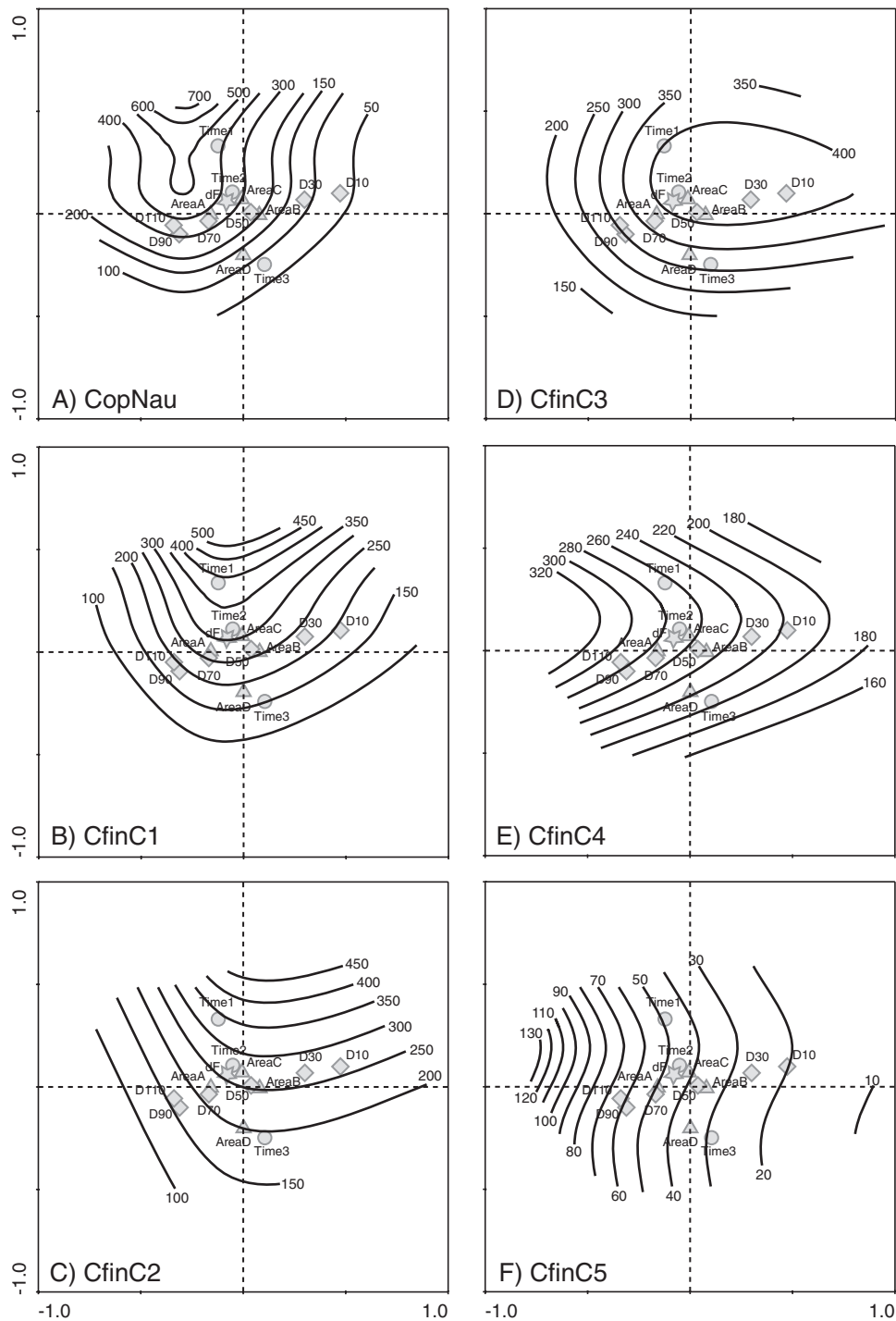


Fig. 4. Correspondence analysis (CA) ordination biplot of axes I and II with a generalized additive model (GAM) fitted to the abundance of (A) Copepod nauplii and *Calanus finmarchicus* copepodite stages (B) CI, (C) CII, (D) CIII, (E) CIV and (F) CV ($n = 30$ stations \times 6 depth intervals). Species abbreviations explained in Table I.

clearly the most numerous and important species in this area. Although *C. finmarchicus* overwinters and spawn on the shelf and in fjords, advection from off-shelf waters

probably contributes to a steady on shelf seeding (Falkenhaug *et al.*, 1997b). This advection varies considerably, and may contribute to an order of magnitude

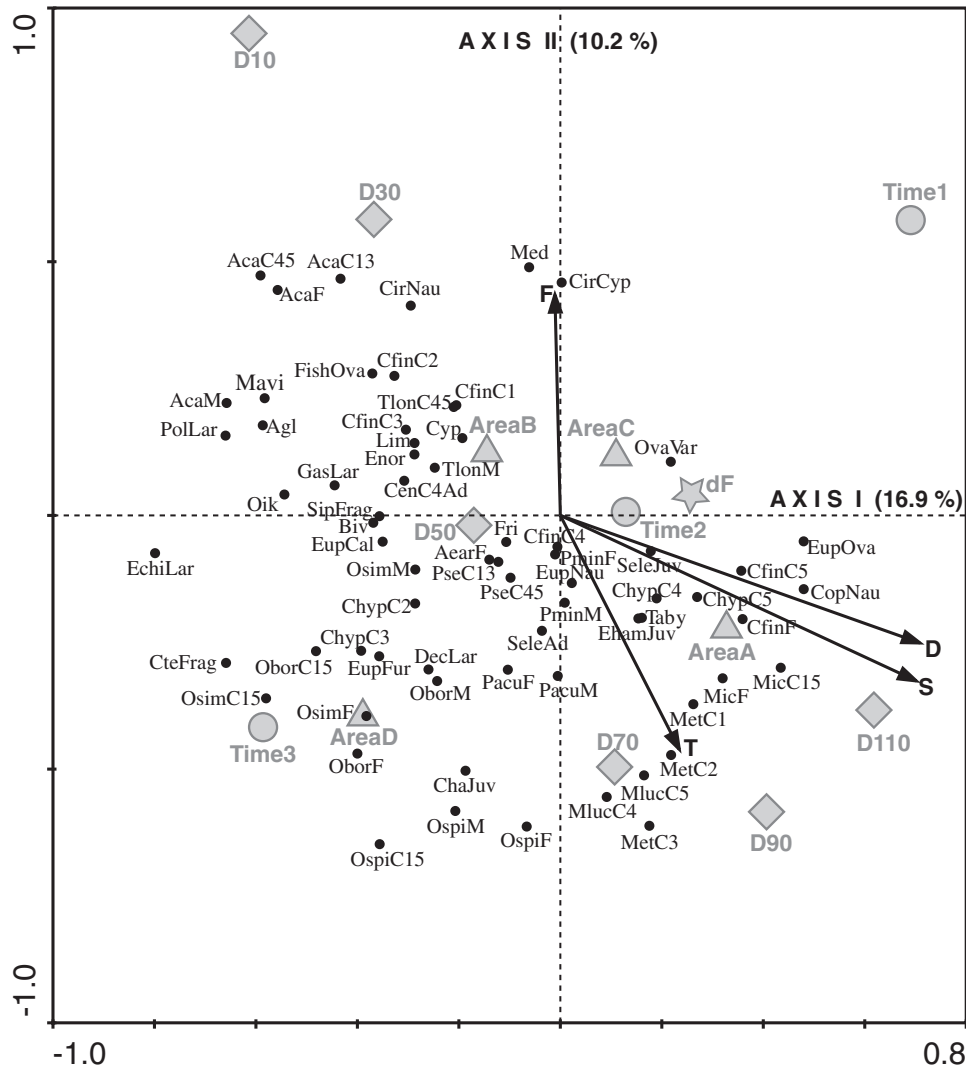


Fig. 5. Redundancy analysis (RDA) ordination biplot of axes I and II relating abundance variations in zooplankton species to areas, depth intervals, times, blooming conditions and environment (temperature, salinity, density and fluorescence) ($n = 30$ stations \times 6 depth intervals). Species abbreviations explained in Table I.

difference in population size between years (Edwardsen *et al.*, 2003a).

The abundance of capelin larvae and the neritic components of zooplankton covaried in space and time. Some of the neritic zooplankters, such as the

invertebrates cyphonautes (free-swimming larvae of Bryozoa), *Limacina* spp. (shelled pteropod), polychaete larvae, bivalves and cirripedia nauplii, might be prey for newly hatched capelin larvae (Moksness, 1982; Pedersen and Fossheim, in prep.). Other prey candidates

Table III: Percentage of variance in species data explained and species–environment correlations by axes I–IV in redundancy analysis (RDA) in Fig. 5

Axis	1	2	3	4
Percentage explained	16.9	10.2	5.8	2.2
Species–environment correlations	0.90	0.80	0.57	0.66
P value	0.002	0.002 (all four axes)		

are the cyclopid species *O. similis* CI-V and *O. borealis* F with abundance maxima overlapping with capelin larvae. This overlap was due to a partial similarity in depth distribution, since the common cyclopoids appear to be distributed independently of the water types found in the study area. *O. similis* CI-V and *O. borealis* F increased in abundance through time, indicating a population response, which is expected for this time of the season in high latitudes (Tande *et al.*, 2000), since the smaller copepods have higher growth and development rates in the pre-bloom phase (Pedersen *et al.*, 1995), and become numerically more important in summer (Lie, 1965).

First feeding capelin larvae are generally thought to prey upon copepod nauplii (Karamushko and Reshetnikov, 1994), and we expected to find a positive relationship between the two. In our study, however, the abundance profiles show no association between capelin larvae and copepod nauplii, and questions a predator–prey link between these two groups. The decoupling of nauplii and capelin larvae may also be influenced by slight differences in depth distribution of the two groups, where copepod nauplii have a deeper depth preference than capelin larvae. This is supported by the close association between copepod nauplii, greater depths and higher salinity (see Fig. 5), which indicate a stronger association to oceanic water masses for copepod nauplii compared to capelin larvae. The observed mismatch in abundance overlap between capelin larvae and copepod nauplii may also be due to heavy predation from capelin larvae, but the predation pressure from a single larval fish species is rarely substantial enough to cause density-dependent effects on their prey (Pepin and Penney, 2000). Additionally, stomach analysis of the newly hatched capelin larvae showed only occasional feeding on copepod nauplii (Pedersen and Fossheim, 2006).

Our analyses demonstrated that copepod nauplii have similar abundance profiles as *C. finmarchicus* CI-CII. Although the abundance estimates do not mirror stage specific mortalities, due to possible biased sampling by MOCNESS (Edwardsen *et al.*, 2003b), the isolines of abundance decline from time 1 to time 3. This is in harmony with a developing cohort of *C. finmarchicus*, and we are therefore confident that this must be the recruiting generation in May 2001. Copepod nauplii are associated with oceanic waters together with, amongst others, *C. finmarchicus* CIV and CV. The water mass separation of copepod nauplii from *C. finmarchicus* CI-CIII may indicate another burst of nauplii on the way in oceanic waters in the study area outside Porsanger in May 2001. A new spawning event in the incoming oceanic water masses, either from *C. finmarchicus* or from other copepod species, cannot be ruled out.

This study has shown that the variation in the species and environment data can be linked to some important

environmental and biological processes. The advection of Atlantic water onto the Barents Sea continental shelf leads to different assemblages of zooplankton found in different water masses. Through time, these water masses are mixed (Pedersen *et al.*, 2005), probably creating new food web links between species from the two different water masses. Some biological–environmental interactions have also been documented (Fossheim *et al.*, 2005), but further investigations are warranted. This study has also demonstrated that capelin larvae hatch in coastal waters and are associated with coastal zooplankton. We interpret this as a lack of coupling between capelin larvae and copepod nauplii (Pedersen and Fossheim, in prep.), which provide evidence that capelin larvae are released into a prey environment in which *Calanus* is not an important player in shaping their initial success, but rather base their foraging on smaller prey organisms more frequently found among coastal zooplankton.

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